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INFORMATION CAPACITY OF EYES

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Abstract—The capacity of an eye to perceive the visual environment is quantified by determining the number of different pictures that can be reconstructed by its array of photoreceptors. There is an optimum density of photoreceptors for each mean luminance and contrast. This is determined by the wave and particle nature of light (diffraction and photon noise). Anatomical and psychophysical data are consistent with the hypothesis that the human retina maximizes the reconstruction of different pictures over the range in luminance required for day and night vision.

I. INTRODUCTION

The perceptive powers of an animal's visual system are determined by two types of constraints. The first is the set of optical factors that determine the quality of the retinal image, while the second class covers all considerations of neural processing of the image. In this study, we set out to derive a measure of optical quality of retinal image that takes into account the two fundamental limiting factors, photon noise and pupil diffraction.

It has long been appreciated that the wave and particle nature of light, as manifested by pupil diffraction and photon noise, represent fundamental limitations to an animal's resolving power (Barlow, 1964). For example, on the one hand, pupil diffraction limits the highest spatial frequency passed by the dioptrics and thus sets the maximum photoreceptor grain (Westheimer, 1972), while, on the other hand, to combat photon noise, a minimum intensity is required for threshold resolution of this highest frequency (Snyder and Miller, 1977). Our purpose is to marry these two limitations in order to obtain a quantitative measure of spatial resolving power.

By employing elementary concepts of information theory we demonstrate how photon noise and pupil diffraction can interact to limit the amount of information available to the visual system. Furthermore, our method of analysis enables one to appreciate the roles played by photon noise and diffraction at any intensity and makes it quite clear that the information content of the retinal image depends upon the manner in which photoreceptors sample the spatial distribution of photon absorptions.

II. CONCEPT OF SPATIAL INFORMATION (PICTURE RECONSTRUCTION)

Every animal's visual system must reconstruct its visual environment from an array of retinal intensity measurements. These measurements are made by individual samplers which we will call photoreceptors. Our idealized photoreceptors are assumed to have photon capture areas which do not overlap, but they differ from physiologically characterized rods and cones in three critical ways. (1) The photoreceptors are linear photon counters at all intensities. (2) They count the photons incident over retinal areas greater than those covered by single inner segments and in this sense resemble rod pools. (3) Ideal photoreceptors count the photons incident in a fixed time interval, whereas real photoreceptors do not.

These ideal photoreceptors reconstruct the spatial distribution of an environmental intensity pattern as an array of intensity measurements and it is convenient to think of this as a checker-board made up of many squares. It is clear that the larger the number of photoreceptors in a given field of view, the better is the ability of this array to reconstruct spatial detail.

However, this spatial detail will be completely lost if each photoreceptor produces a photon count that is not significantly different from that of its neighbours (all the squares now have the same gray tone). The photoreceptors must also have contrast sensitivity which is determined by the number of different intensity levels that can be reliably distinguished across the array. At first sight, it might appear that there is no restriction upon the number of intensity levels that can be distinguished; however, we show below that the quantum nature of light, and in particular photon noise, sets a lower limit to the intensity levels that can be reliably discriminated. The more photons captured by the photoreceptor, the greater the number of distinguishable intensity levels and so the greater the contrast sensitivity of the array. Thus, in summary, both space and intensity are quantized by the photoreceptor array of the eye.

It is clear that this quantization of space and intensity determines the quality of the image that is reconstructed. As one increases the number of photoreceptors per field of view, one gains more potential for monitoring fine spatial detail, but, because each photoreceptor now counts fewer photons, there is a fall in the number of distinguishable intensity levels. In view of this inevitable competition between fine spatial detail and contrast sensitivity, what is the most appropriate number of photoreceptors to place in a field of view? The answer clearly depends upon the

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Table 1. List of important symbols

$\Delta\phi$ = angular center-to-center separation of photoreceptors (degrees).
$\Delta\rho_r$ = angular diameter of a photoreceptor's inner segment (degrees).
$\Delta\rho_l$ = angular width of the point spread function of the lens–pupil at 50% maximum (see Fig. 3) (degrees). When the dioptrics are diffraction limited, $\Delta\rho_l = \lambda/D$, where λ is the wavelength in vacuum and D is the entrance pupil diameter.
$(\Delta\rho)^2 = (\Delta\rho_l)^2 + 0.38(\Delta\rho_r)^2$ = total half width of point spread function at photoreceptor (degrees).
C = mean contrast of a random two-dimensional distribution of light intensity in the object world (see Fig. 1).
$\tilde{I}$ = intensity parameter. Number of photons absorbed by the photoreceptor array per square degree of object field and per integration time of the eye due to a uniform source, infinite in extent.
(1) $\tilde{I} = (\pi/4)\, \bar{I}\eta\Delta t$; (degrees)$^{-2}$.
(2) $\bar{I}$ = mean number of photons entering the eye per square degree of object field per second (degrees^{-2} sec^{-1}) ($\bar{I}$ is proportional to the pupil area).
(3) η = quantum efficiency, i.e. the fraction of photons entering the pupil that are counted by the photoreceptors.
(4) Δt = integration time (effective shutter time) of the eye (sec).
$\bar{N}$ = mean numbers of photons absorbed by a photoreceptor per integration time of the eye due to a uniform source, infinite in extent $\bar{N} = \tilde{I}(\Delta\rho_r)^2$.
H = information capacity per square degree of object field, defined here to be the natural logarithm of the number of different pictures that can be reconstructed by an array of photoreceptors.
(1) $H = n_p \ln n_i$ (degrees^{-2}).
(2) n_p = the number of photoreceptors per square degree of object field [equation (2)] (degrees^{-2}).
(3) n_i = the number of different intensity levels that can be distinguished by the photoreceptor array [equation (5c)].

total number of photons available to the array and also on the type of task one requires of the array. We propose that a measure of performance which specifically favours neither contrast sensitivity nor the resolution of spatial detail, is the number of pictures that the photoreceptor array can reconstruct.

Assuming that there are n_p photoreceptors per field of view, each one with *one* of n_i possible intensity levels, the *maximum* number of pictures that can be reconstructed by the photoreceptors is $n_i^{(n_p)}$. Now it follows from the classical arguments of information theory (Goldman, 1953; Pierce, 1961) that the logarithm of the *maximum* number of *different* pictures that can be reconstructed, per field of view, is the *spatial information capacity of the eye*, denoted here as H.

$$H = \ln n_i^{(n_p)} = n_p \ln n_i, \tag{1}$$

where ln is to the base e. By using the logarithm of the number of pictures, we preserve the intuitive notion that doubling the number of photoreceptors per field of view n_p, doubles the spatial information capacity H of an eye.

Armed with the essential concept of picture making, we next determine n_p and n_i from the physical parameters of the eye. For simplicity, we assume that the photoreceptors are arranged in a square lattice. The results for a hexagonal lattice are similar (Snyder and Miller, 1977) and are stated in Appendix A2. The number of photoreceptors per square degree of object space, n_p, is

$$n_p = 1/(\Delta\phi)^2, \tag{2}$$

where $\Delta\phi$ is the angular center-to-center separation of photoreceptors.

III. NUMBER OF INTENSITY LEVELS THAT CAN BE DISTINGUISHED RELIABLY WITHIN THE MOSAIC OF PHOTORECEPTORS, n_i

Two phenomena limit the number of intensity levels that can be reliably distinguished by the array of photoreceptors n_i. They are noise, which in this case is due to the quantum nature of light, and imperfections in the optics which cannot be reduced below the diffraction limit that is determined by the wave properties of light and the diameter of the pupil. We now consider their effects in turn.

(1) *Limitations of photon noise to the number of discriminable intensity levels* n_i

Photons are absorbed at random. Consequently, any uniform light source will appear non-uniform to an array of photoreceptors, as shown in Fig. 1. The random fluctuations in photon counts across many photoreceptors are measured as a standard deviation, σ_{noise}, given by

$$\sigma_{noise} = \sqrt{\bar{N}}, \tag{3}$$

where $\bar{N}$ is the mean number of photons captured by individual photoreceptors during one integration time (Barlow, 1964; Rose, 1973). If two intensity levels are to be distinguished reliably, then they must differ by an amount that is significantly greater than the noise level. For our analysis, we choose a separation of $2\sigma_{noise}$ for reliable discrimination. This is the usual criterion adopted by communications engineers because it can be shown to give the best trade-off between reliability and number of intensity levels (Carslon, 1975). Thus n_i is found by determining the number of intervals of $2\sigma_{noise}$ that fit into the range of photon counts that occurs across the mosaic.

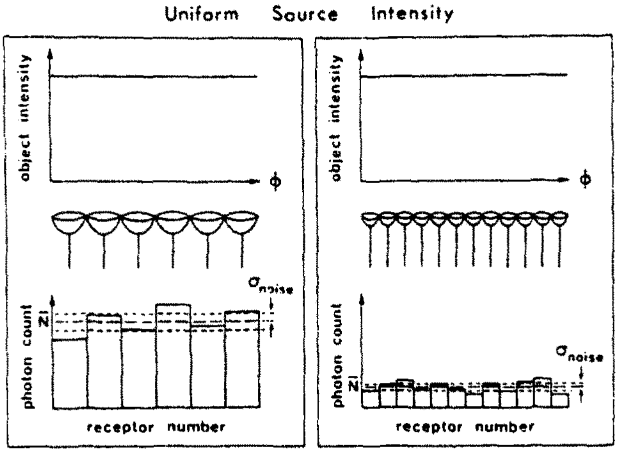

Fig. 1. The fluctuation in photon counts that results from the random arrival of photons during one integration time. The object is a uniform source, infinite in extent. The left and right hand figures illustrate the effect of having large or small photoreceptors. (See also Fig. 3).

To determine the number of possible intensity levels n_i, we must decide on the range in intensity that is to be found across the mosaic. We are reminded that our expression for spatial information capacity H, given by equation (1), is based on the *maximum* number of pictures that photoreceptors can reconstruct. It is necessary to know what distribution

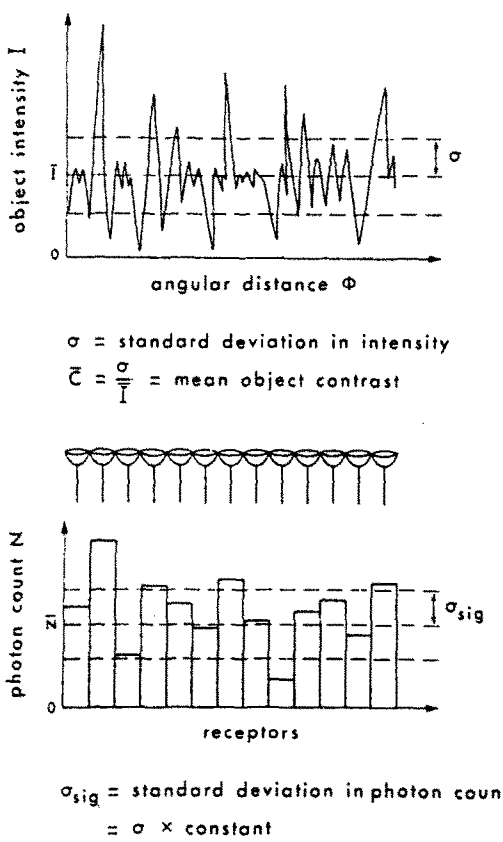

Fig. 2. Spatial distribution of photon counts N by an array of photoreceptors due to a random distribution of object intensity I. The effect of noise has been intentionally neglected but is included in Fig. 3.

of object intensities would produce this maximum. From information theory (e.g. Pierce, 1961) we learn that a random scene fulfills the requirement, i.e. a scene containing objects of random contrast and random size, or identical size at random distances from the eye. Such a scene is the epitome of the unexpected since every spatial frequency has equal importance. The spatial information capacity H of an eye is therefore equivalent to the amount of information that can be extracted from a random scene. *Accordingly, we determine the number of possible contrast levels that exist when the object intensity is random, as in Fig. 2.*

In the absence of photon noise, the standard deviation σ_{sig} in photon counts, due to the random scene in Fig. 2, is

$$\sigma_{sig} = \bar{N}\bar{C}, \tag{4}$$

where $\bar{N}$ is the mean number of photons absorbed by the individual photoreceptors and $\bar{C}$ is the mean contrast of the object intensity distribution. In the presence of noise (Fig. 3), twice the standard deviation in photon counts is given by $2(\sigma_{sig}^2 + \sigma_{noise}^2)^{\frac{1}{2}}$ [remembering that variances and not standard deviations must be summed (Goldman, 1953)]. Dividing this expression by $2\sigma_{noise}$ gives the number n_i of possible intensity levels

$$n_i = \{1 + \sigma_{sig}^2/\sigma_{noise}^2\}^{1/2}, \tag{5a}$$

$$= \{1 + \bar{N}\bar{C}^2\}^{1/2}, \tag{5b}$$

assuming photon noise is the only limitation. This expression is inaccurate for small values of $\bar{N}$. In Appendix C, we derive a more accurate form:

$$n_i = \left\{1 + \frac{(\bar{N}\bar{C})^2}{\bar{N}+1}\right\}^{1/2} \tag{5c}$$

We next examine how imperfect optics modify this result.

(2) *Limitations of imperfect optics plus photon noise to the number of discriminable intensity levels*

In order to appreciate how imperfect optics limits the number of intensity levels, we must first discuss

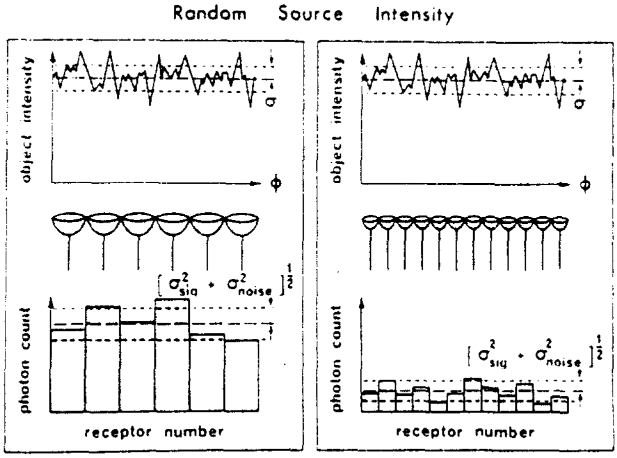

Fig. 3. The effect of noise on the spatial distribution of photon counts in an array of photoreceptors that are sampling a random distribution of object intensities. Large photoreceptors receive on average, more photons than smaller ones and have, therefore, a better signal to noise ratio, but this is achieved at the expense of resolution of fine spatial detail.

some basic concepts of optical filtering (Goodman, 1968). The most useful way to quantify the effect of imperfect optics is by the demodulation of a spatial sinusoid as it passes through each component part of the optical system (Fig. 4). In particular, we use the modulation transfer function $M(\nu)$ or MTF to characterize the modulation of a spatial sinusoid of unity amplitude and frequency ν after passing through all components of the imaging and sampling system. The MTF of the lens–pupil is $M_l(\nu)$, while the MTF due to the finite diameter of the photoreceptor is $M_r(\nu)$. Thus, as shown in Fig. 4, the modulation that appears across the array of photoreceptor cells is a quantized version of $m\ M_l M_r$, where m is the object contrast or modulation. The highest spatial frequency passed by a pupil of diameter D is $\nu = D/\lambda$, where λ is the wavelength of light in vacuum (Goodman. 1968).

It is intuitive, from Fig. 5, that the angular spacing of photoreceptors can set the highest spatial frequency ν_s that is reconstructed by the array of photoreceptors. We call ν_s the sampling frequency of the photoreceptor array where

$$\nu_s = \text{sampling frequency} = 1/2\Delta\phi, \qquad (6)$$

assuming a square array of photoreceptors. The case for a hexagonal lattice is discussed in Appendix A2.

A random distribution of object intensities contains all spatial frequencies, equally weighted (O'Neill. 1963). In Appendix A, by using Fourier analysis of random distributions, we have shown that the presence of imperfect optics reduces the number of poss-

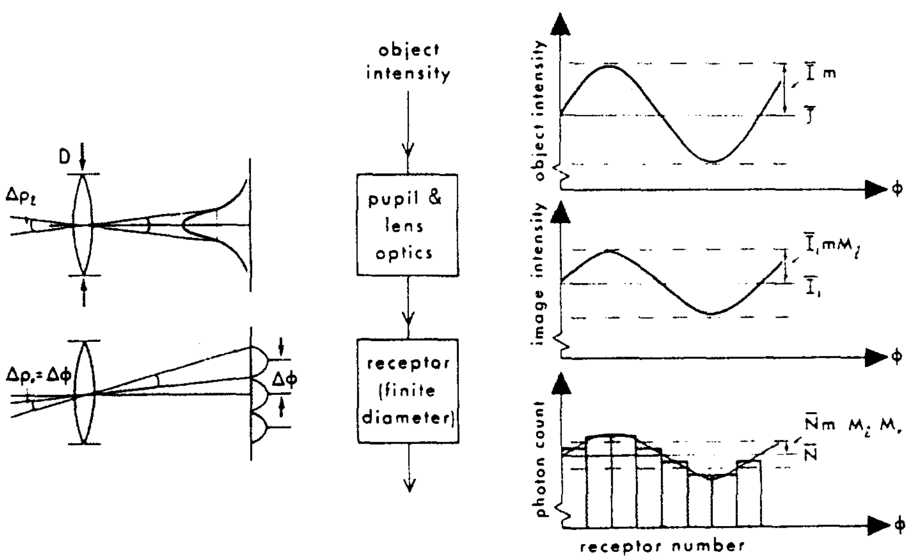

Fig. 4. The effect of the dioptrics and finite photoreceptor diameter on the modulation of a sinusoidal grating of spatial frequency ν. The object modulation is m, the modulation transfer function of the lens–pupil and photoreceptor are M_l and M_r respectively.

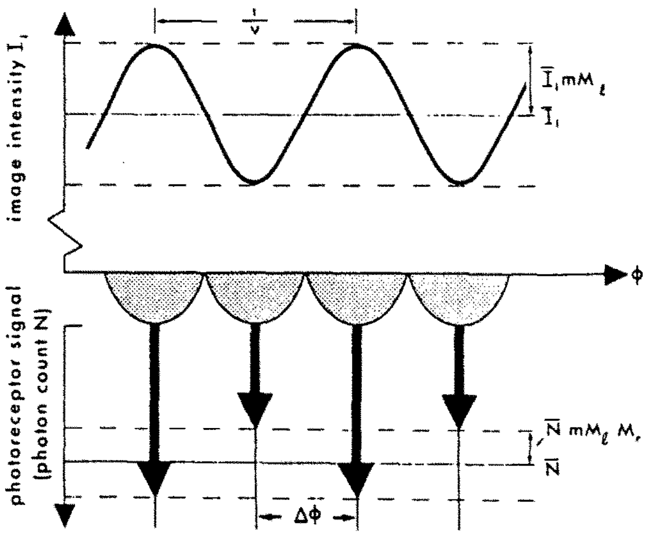

Fig. 5. Minimum number of photoreceptors per field of view necessary to reconstruct a sinusoidal grating of spatial frequency ν, where M_l and M_r are the modulation transfer functions of the lens–pupil and photoreceptors respectively.

ible intensity levels n_i from that given by equation (5c) to

$$n_i = \left\{1 + \frac{(\bar{N}\bar{C})^2}{\bar{N}+1} M(\nu_s)\right\}^{1/2}, \tag{7}$$

where $M = M_l M_r$. The greater ν_s, the smaller $M(\nu_s)$, and hence the fewer intensity levels that can be distinguished.

IV. EYE DESIGN AND SPATIAL INFORMATION CAPACITY

We can now derive the spatial information capacity of a photoreceptor array as a function of intensity, photoreceptor size and performance of the dioptrics. From equations (2) and (7) we can rewrite equation (1), leading to an expression for the spatial information capacity H

$$H = \frac{1}{(\Delta\phi)^2} \ln \left\{1 + \frac{(\bar{N}\bar{C})^2}{\bar{N}+1} M(\nu_s)\right\}^{1/2} \tag{8}$$

Expressions for $M(\nu_s)$, the total MTF at the sampling cut-off frequency, and $\bar{N}$ the mean photon capture are derived in Appendices C and D, respectively, leading to

$$M(\nu_s) \cong 0.7 \exp\left[-0.89\left(\frac{\Delta\rho_l}{\Delta\phi}\right)^2\right] \tag{9}$$

$$\bar{N} = \tilde{I}(\Delta\phi)^2, \tag{10}$$

where the intensity parameter $\tilde{I}$ is defined in Table 1, $\Delta\rho_l$ is the half width of the point spread function of the lens–pupil system when the system is limited by diffraction alone, $\Delta\rho_l = \lambda/D$. We have set the angular light capture diameter of the photoreceptor $\Delta\rho_r$ equal to the angular photoreceptor spacing $\Delta\phi$ in equation (9) and (10), because this is shown in Appendix A5 to give the highest possible information capacity, H, for non-overlapping receptive fields.

We now solve equation (8) to determine the photoreceptor spacing $\Delta\phi$ that maximizes the information capacity of an array of identical photoreceptors lying in the image plane of a lens–pupil system of diameter, D. We find that there is a different optimum angular

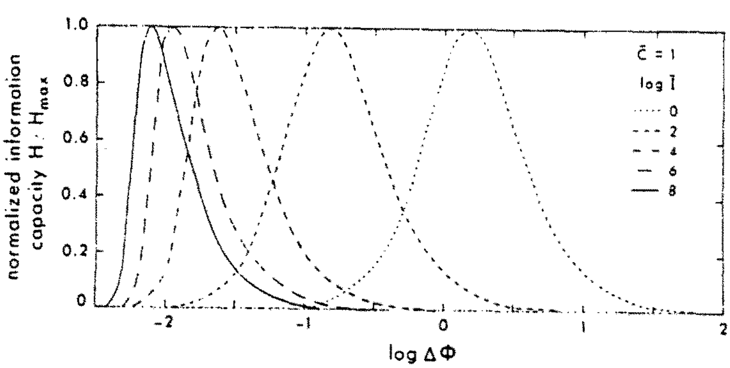

Fig. 6. Dependence of the information capacity H on the photoreceptor spacing $\Delta\phi$ for a number of values of the intensity parameter $\tilde{I}$ (see table 1) when the mean object contrast $\bar{C} = 1$. The results are found from eq. (9) with $\Delta\rho_l = 0.016°$ which corresponds to a diffraction limited pupil of diameter 2 mm when $\lambda = 550$ nm.

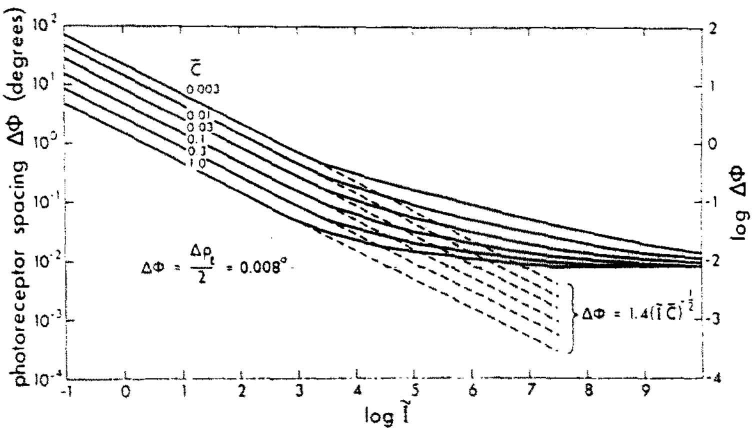

Fig. 7. Photoreceptor spacing $\Delta\phi$ that maximizes the information capacity H for a given intensity parameter $\bar{I}$ (see table 1), mean object contrast $\bar{C}$, and $\Delta\rho_l = 0.016°$. The dashed curve gives the optimum $\Delta\phi$ when only noise and the finite photoreceptor diameter limit $\tilde{H}$ (see appendix A6).

spacing of photoreceptors, $\Delta\phi$, for each value of the intensity–contrast parameter $\bar{I}\,\bar{C}^2$, e.g. see Fig. 6. In Fig. 7 we have plotted these optimum $\Delta\phi$s vs $\bar{I}$ for a range of contrasts. This curve illustrates several important features. At low values of $\bar{I}$, the optimum photoreceptor spacing is given by $1.4(\bar{I}\,\bar{C})^{-1/2}$, i.e. it is independent of pupil diffraction and follows the well-known square root law of an ideal detector (Barlow, 1964; Rose, 1973). As the intensity increases, the optimum spacing approaches the limit set by pupil diffraction, i.e. $\Delta\phi = (\Delta\rho_l/2) \geqslant \lambda/2D$ for a square array. For a hexagonal array of photoreceptors $\Delta\phi = \lambda/D\sqrt{3}$ (Snyder and Miller, 1977). No additional information is gained by having a value of $\Delta\phi$ smaller than that limited by diffraction.

A minimum intensity $\bar{I}$ is required if the minimum, dioptric limited, photoreceptor spacing $\Delta\phi = \Delta\rho_l/2$ is to provide optimum information capacity, and in Appendix A7 this is shown to be

$$\log \bar{I}(\bar{C}\,\Delta\rho_l)^2 \cong 4.28, \tag{11}$$

where $\Delta\rho_l$ is in degrees. Note that because $\bar{I}$ is proportional to D^2 (Table 1) the corneal intensity required to attain the diffraction limit is independent of pupil size.

Figure 8 shows the relation between the intensity parameter $\bar{I}$ and the mean number of photons $\bar{N}$ that must be counted by the individual photoreceptors if the retina is to perform at optimum. At the high intensity limit, where the photoreceptors have the minimum spacing $\Delta\phi = \Delta\rho_l/2$, then from Appendix A7 we find that each photoreceptor must count, on average, at least $4.8 \times 10^3/\bar{C}^2$ photons. This compares with an average count given by $\bar{N} \cong 2/\bar{C}$ when intensity is comparatively low.

Figure 9 represents a plot of the maximum information capacity $H_{\max}$ vs $\bar{I}$. The greater $\bar{I}$, the greater $H_{\max}$. Note that information capacity still increases with intensities greater than that required for photoreceptors to be spaced at the diffraction limit $\Delta\phi = \Delta\rho_l/2$, because the number of contrast levels n_i is then proportional to $\sqrt{\bar{I}}$.

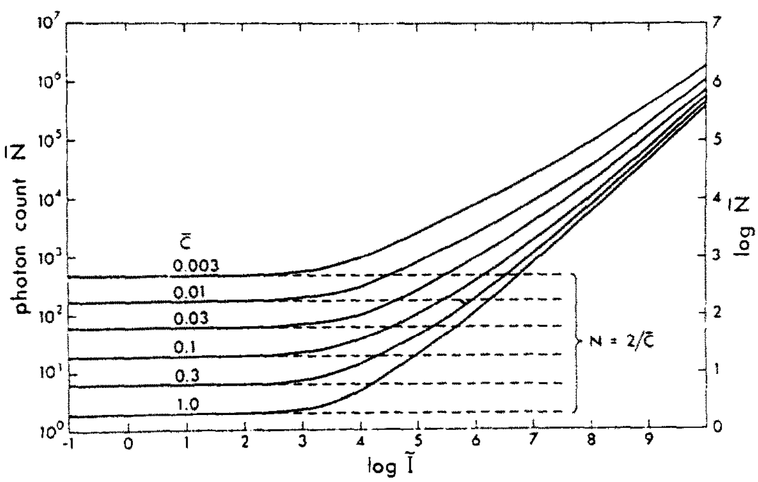

Fig. 8. Mean photon count $\bar{N}$, per integration time of the eye, by the individual photoreceptors when they have the optimum separation for maximum information capacity H. The intensity parameter $\bar{I}$ is defined in table 1.

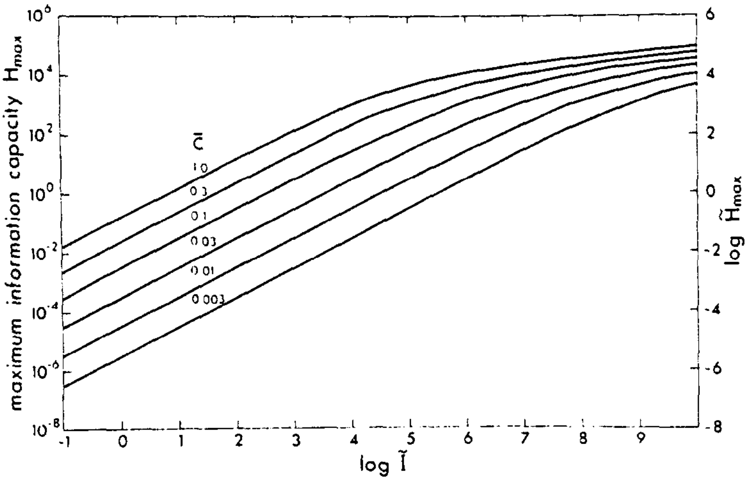

Fig. 9. The maximum information capacity H_{max}, i.e. H for the optimum $\Delta\phi$, vs the intensity parameter $\bar{I}$ (see table 1).

IV. DISCUSSION

We have derived the information capacity of arrays of photoreceptors in terms of the fundamental physical restrictions placed upon them by the wave and particle nature of light. Information capacity is a measure of the quality of the image that depends upon the manner in which photon hits can be counted. It is not itself affected by subsequent neural processes, although the extent to which transduction and neural interactions change the information capacity of the system at the level at which they operate is well worth further investigation.

Our derivation of information capacity is a general metric applicable to any photoreceptor array. The random pattern used as a test object is the most general available because it contains all possible intensity patterns, and the analysis places no deliberate emphasis on any one aspect of acuity, such as spatial acuity. It only seeks out the potential for receiving novel images. Although other quality factors have been used for evaluating the performance of electro-optical systems, these are shown in Appendix A4 to be special limiting cases of our number of pictures criterion.

We have demonstrated how lens imperfections and photon noise limit the information capacity H (picture reconstruction ability) of an array of ideal photoreceptors. At low intensities, random fluctuations in photon counts due to the quantum nature of light limit performance. An absolute minimum of two photons must be counted on average by at least one photoreceptor, in the integration time of the eye, if the array is to carry reliable information on two different intensity levels ($n_i = 2$) (see Appendix C). From equation (1), it is clear that, unless two levels in intensity are distinguishable, the information capacity H is zero. At high intensity, the smallest angular spacing of photoreceptors, $\Delta\phi$ (highest acuity), is limited by the quality of the optics, and ultimately by the wave nature of light. If the lens–pupil is diffraction limited, then D/λ is the highest spatial frequency that can be reconstructed by an array of photoreceptors. The *optimum* spacing of photoreceptors is then about $\Delta\phi = \lambda/2D$, where λ is the wavelength of light and D the pupil diameter. Thus both the photon noise and the diffraction limits are an integral part of our expression for information capacity H given by equation (8).

Previous theoretical studies have considered how either diffraction or random photon fluctuations limit visual discrimination at threshold (e.g. Hecht, Shlaer, and Pirenne, 1942; De Vries, 1943; Rose, 1948; Barlow, 1964; Campbell and Green, 1965). We have investigated how both factors act together to limit the ability of the photoreceptor array to reconstruct different pictures by finding the photoreceptor spacing, $\Delta\phi$, that maximizes the information capacity H at each mean object intensity and contrast.

Since, as shown in Figs. 6 and 7, there is an optimum photoreceptor spacing $\Delta\phi$ for each mean object intensity and contrast, a retina must have many different receptor spacings if it is to perform optimally (for picture reconstruction) over a wide range of intensity and contrast. We illustrate this for the human retina.

Figure 10 shows the photoreceptor spacing necessary for a given region of the human retina to maximize the number of different pictures that its photoreceptors can reconstruct. The curves are taken from the data of Fig. 7, while the integration time for the rods and cones and the details of converting from $\bar{I}$ to trolands are presented in Appendix D.

It is acceptable to assume a diffraction limited pupil of 2 mm in diameter because in the human eye, the modulation transfer function is relatively insensitive to changes in pupil diameter. As the diffraction blur decreases, aberrations increase (Campbell and Gubisch, 1966; Van Meeteren, 1974).

In the most densely packed region of the human fovea, the minimum angular spacing of cones is approximately $\Delta\phi = 0.008°$ (Pirenne, 1966), which is consistent with the optimum acuity of humans measured psychophysically (e.g. Green, 1970). A minimum retinal illuminance of T td given by

$$\log T\bar{C}^2 = 4.4 \tag{12}$$

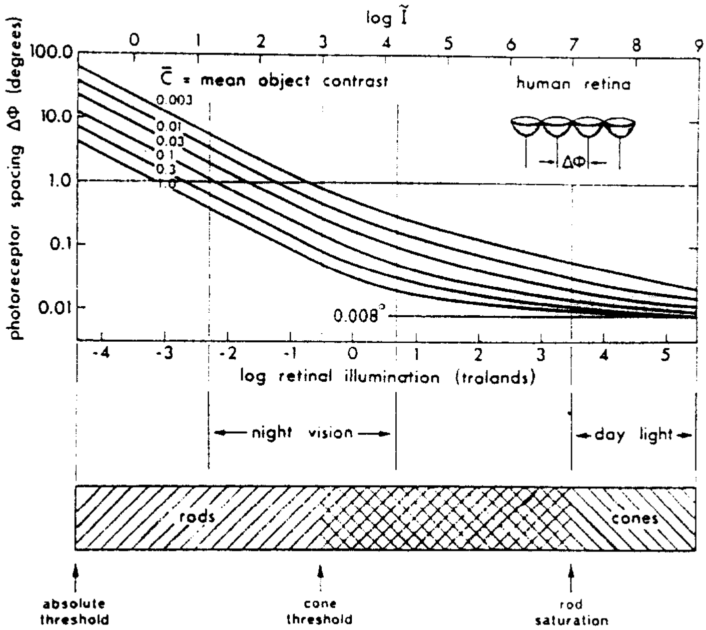

Fig. 10. Angular center to center spacing of photoreceptors $\Delta\phi$ that is necessary to maximize the picture making ability of the human retina for a given mean retinal illumination and mean object contrast $\bar{C}$. The curves are calculated from eq. (9) with the conversion from the intensity parameter $\tilde{I}$ (see table 1) to trolands in Appendix D. The values for: absolute threshold (10^{-6} cd/m^2 = -0.9 log td) is taken from Pirenne (1962), page 129; cone threshold (-0.5 log td), Daitch and Green (1969); Rodieck (1973), p. 455; rod saturation (-3.5 log td), Pirenne (1962), p. 165. The values for night vision (10^{-4} to 10^{-1} cd/m^2 = -2.3 to -0.7 log td) and daylight (10^3 to 10^5 cd/m^2 = 3.5 to 5.5 log td) refer to retinal illumination due to reflections from a white surface (Le Grand, 1968, p. 84, and Pirenne, 1962, p. 10).

is required if the centermost region of the human fovea is to maximize picture reconstruction. [This result follows from equation (11) and equation (D4) of Appendix D.] For values of $\bar{I}$ below this minimum, a less dense sampling distribution will provide a greater number of pictures. For example, the largest spacing of cones in the rod-free region of the fovea is about $\Delta\phi = 0.014°$ (Pirenne, 1966). According to Fig. 10, this region of the retina requires about 1.5 log td to function at optimum when the mean contrast $\bar{C} \cong 1$, while 5.5 log td are necessary when $\bar{C} \cong 0.01$.

We see from Fig. 10 that photoreceptors with large inner segments (e.g. $\Delta\phi \cong 1.0°$) are necessary for maximum picture reconstruction at low retinal illumination. Outside the fovea, rods greatly outnumber cones in the human retina. However, the diameter of rod inner segments is about the same as the central-most foveal cones, so that the results of Fig. 10 do not agree with the spacing of anatomical photoreceptors in the peripheral retina. Nevertheless, because of neural summation, the retina may function as though it were constructed from effective large diameter photoreceptors. The fall in acuity and rise in sensitivity in the peripheral retina supports this possibility.

Rod monochromats have their highest acuity consistent with an angular center-to-center spacing of effective photoreceptors with $\Delta\phi \cong 0.1°$ (Hecht, Shlaer, Smith, Haig and Peskin, 1948). Rodieck (1973, p. 454) points out that this angular distance is the same size as the dendritic spread of human rod bipolars and that, because the overlap of the dendritic fields of adjacent primate rod bipolar cells is small, "the rod bipolars behave (with reference to summation) as though there existed a single broad photoreceptor of this diameter". Thus, the minimum effective rod diameter in the human retina is assumed to be no less than $\Delta\phi \cong 0.1°$.

The largest effective photoreceptor diameter can be inferred by acuity measurements in the most peripheral regions of the human retina. At an eccentricity of 70° (temporal on retina), the highest photopic acuity corresponds to $\Delta\phi \cong 0.5°$ for a grating test pattern and $\Delta\phi \cong 0.8°$ for a Landolt C test object (Weale, 1956; Pirenne, 1962; Le Grand, 1967). Furthermore, Mandelbaum and Sloan (1947) show that the acuity of the peripheral retina (beyond 20° eccentricity) is relatively insensitive to changes in retinal illuminance, as in the rod monochromat studied by Hecht *et al.* (1948). We conclude that the largest effective photoreceptor diameter in the human retina is somewhere between $\Delta\phi = 0.5°$ and $\Delta\phi = 0.8°$, i.e. about 100 times that of the central-most foveal cone. A 100-fold range in effective photoreceptor diameters is seen from Fig. 10 to adequately provide the human with maximum information capacity for night and day vision.

From the theory of this paper, it is reasonable to suppose that an arhythmic animal [an animal active both at night and day (Walls, 1942)] should have a greater range in effective photoreceptor spacing than either a diurnal or nocturnal animal. Evidence for this possibility is suggested by comparing ganglion cell densities within these three types. Hughes (1976) has shown that nocturnal animals have a low ganglion cell density with little centro-peripheral density gradient, while diurnal animals are characterized by a high ganglion cell density also with little centro-peripheral density gradient. Arhythmic animals, like man, have a high centro-peripheral density gradient (Van Buren, 1963; Hughes, 1976).

We have shown that if an eye is to have optimum information capacity over a range of intensities and contrasts, then it must possess a range of effective photoreceptors of different sizes. Both anatomical and psychophysical data are consistent with the hypothesis that the human retina has this ability. We now examine what the application of information theory to photon sampling can and cannot tell us about the way to arrange effective photoreceptors of different sizes across the retina.

An eye only realizes its full information capacity at any one mean intensity if it has an array of effective photoreceptors of the correct size covering its entire field of view. Thus, to obtain as many pictures as possible over a large intensity range, a retina would require effective photoreceptors of all required diameters in all retinal areas. This could be achieved neurally, by setting the anatomical photoreceptors at the diffraction limit of the pupil and sending the photon count of each photoreceptor into a large number of parallel summation pools. It is possible that several parallel pools, operating simultaneously, would further increase the picture-making capacity, but this point requires further analysis. Many retinas do have small photoreceptors spaced at, or close to, the limit imposed by the resolving power of their dioptrics, but it seems unlikely that many eyes would employ the complete parallel pooling strategy advocated by consideration of total information capacity alone.

Other factors also limit the degree to which a retina can pool signals from its receptors. For example, the large number of neurons required for complete parallel pooling would degrade image quality by thickening the plexiform layers, enlarging the optic disc and increasing the number of blood vessels. A more economical strategy is to use a small number of parallel pools in any one retinal area, each of which can make small adjustments to its capture area as a function of mean intensity. A still greater reduction in the number of neural channels can be obtained by restricting the high-acuity channels, which presumably require the greatest number of neurons per retinal area, to a fovea. This does not mean that the fovea must also sacrifice its potential to make large pools as well.

Finally, we stress again that information capacity is not the only consideration required to come to an understanding of the functional basis of vertebrate retinal organization. For example, elegant and convincing correlations have been made between retinal ganglion cell density and the velocity of retinal image translation during locomotion of an animal through its preferred environment (Hughes; 1976). However, the derivation of information capacity has proved useful in analysing the structure and function of compound eyes (Snyder, Stavenga and Laughlin, 1977), where the spacing of photoreceptors (ommatidia) also determines the optical quality of the lenses. Thus it appears that picture-making capacity is a useful addition to the battery of analytical concepts that are required to understand the function of all visual systems. Hopefully, this type of analysis will contribute to our understanding of the strategies of neural integration which lie beyond photon absorptions.

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APPENDIX A. DERIVATION OF SPATIAL INFORMATION CAPACITY OF EYES

Our purpose is to calculate the information content of the image formed by the array of photoreceptor cells when the object is a two-dimensional random scene. Fourier analysis is used to decompose the object intensity into a superposition of sinusoidal gratings, each of which contains a portion of the information content of the pattern. Then, equation (1) is used to calculate the information content of each differential portion of the spatial frequency spectrum.

We begin with a one-dimensional retina and then generalize to the two-dimensional case.

(A1) *One-dimensional retina*

For the eye to reconstruct a spatial frequency ν, it is intuitive that there must be at least one photoreceptor allocated to each node and antinode of the image intensity pattern (Fig. 5). Thus, the minimum number n_p of photoreceptors per degree of object space required for detecting a spatial sinusoid of frequency ν is

$$n_p = 2\nu. \qquad \text{(A1)}$$

Conversely, for a given angular separation $\Delta\phi$ between photoreceptors, the maximum detectable spatial frequency is $\nu_{max} = 1/2\Delta\phi$. This result is proven by the one-dimensional sampling theorem (Goodman, 1968).

Substituting equation (A1) into equation (1) of the text leads to $H = 2\nu \ln n_i$, where H is the information capacity per degree of object space. The differential amount of information $\mathrm{d}H$ within a small frequency range $\mathrm{d}\nu$ centered about ν is therefore

$$\mathrm{d}H = 2\mathrm{d}\nu \ln n_i(\nu). \qquad \text{(A2)}$$

We must now determine the number of possible intensity levels $n_i(\nu)$ of a spatial sinusoid that can be reliably distinguished. From equation (5a) of the text, we see that n_i depends on the signal to noise ratio $\sigma_{sig}/\sigma_{noise}$ of the photoreceptors.

As shown in Figs. 4 and 5, the signal at the photoreceptor level due to a sinusoidal object intensity is a quantized version of the sinusoid of amplitude $m\,M\,\bar{N}$, where m is the object modulation, $M(\nu)$ the combined modulation transfer function of the lens–pupil system and finite photoreceptor diameter, and $\bar{N}$ is the mean number of absorbed photons. Thus, the signal amplitude is

$$\sigma_{sig}(\nu) = m\,\bar{N}\,M(\nu). \qquad \text{(A3)}$$

In Appendix C, we show that the noise variance can be expressed as the sum of the variance in quantum fluctuations $\bar{N}$ plus the variance in effective intrinsic noise ϵ^2.

$$\sigma_{noise} = (\bar{N} + \epsilon^2)^{1/2}. \qquad \text{(A4)}$$

Since a random signal is composed of all spatial frequencies of equal amplitude (Goldman, 1953), the total information capacity H is found by integrating equation (A2) from $\nu = 0$ to $\nu_{max} = 1/2\Delta\phi$. Thus.

$$H = 2\int_0^{1/2\Delta\phi} \mathrm{d}\nu \ln n_i(\nu). \qquad \text{(A5)}$$

If we assume that the object modulation m is the same for each spatial frequency, then equation (A5) is the information capacity per degree of object space due to a random scene of mean contrast $\bar{C}$, where $\bar{C} = m$.

This is an intuitive derivation. A rigorous treatment requires statistical concepts used in Fourier analysis of filtered random signals and noise (e.g. Goldman, 1953, p. 158; Aseltine, 1958; O'Neill, 1963). Those familiar with these methods will note that the quantity $\sigma^2_{sig}/\sigma^2_{noise}$ is the ratio (power spectrum of signal)/(power spectrum of noise). We have assumed that the object and noise power spectrum are equal and uniform in spatial frequency ν.

(A2) *Two-dimensional retina*

(1) *Square array of photoreceptors.* If we use a rectangular coordinate system, the generalization of the above derivation is straightforward. The number of photoreceptors per square degree of object space required for detecting two orthogonal and phase-independent spatial sinusoids is given by

$$n_p = 4\,\nu_x\,\nu_y, \qquad \text{(A6)}$$

where the subscripts x and y represent the X- and Y-axes of a Cartesian coordinate system. Furthermore, we replace $M(\nu)$ in equation (A3) by the two-dimensional modulation transfer function $M(\nu_x, \nu_y)$ (Goodman, 1968). The two-dimensional equivalent of equation (A5) is

$$H = 4\int_0^{1/2\Delta\phi_x} \mathrm{d}\nu_x \int_0^{1/2\Delta\phi_y} \mathrm{d}\nu_y\, n_i(\nu_x, \nu_y), \qquad \text{(A7)}$$

where $\Delta\phi_x$ and $\Delta\phi_y$ are the spacing of photoreceptors along the X- and Y-axes, respectively, and H is the information capacity per square degree of object space.

We convert equation (A7) to the polar coordinate variable ν, since the integrations are then more easily performed. This gives

$$H = \pi\left(\frac{4}{\pi}\right)\int_0^{1/2\Delta\phi} \nu\,\mathrm{d}\nu \ln\left\{1 + \frac{[\bar{C}\bar{N}M(\nu)]^2}{\bar{N} + \epsilon^2}\right\}, \qquad \text{(A8)}$$

where $(\Delta\phi)^2 = (\Delta\phi_x)^2 + (\Delta\phi_y)^2$ and $M(\nu)$ is the MTF of the total system as derived in Appendix B. The factor $4/\pi$ has been introduced so that the same number of photoreceptors are involved in the calculation based on rectangular coordinates as that in polar coordinates, i.e. when $M = 1$, equation (A8) reduces to $n_p \ln n_i$, where $n_p = 1/(\Delta\phi)^2$.

(2) *Hexagonal array of photoreceptors.* When the photoreceptors are packed in a hexagonal array, the distance between samplers is smaller than in a square array. Replacing $\Delta\phi$ in equation (A8) by $\sqrt{(3)}\,\Delta\phi/2$ then gives the correct result (Snyder and Miller, 1977).

(A3) *Approximate expression for* H

Equation (A8) can be approximated by assuming $M(\nu)$ to be a Gaussian function (see Appendix B) and $[\bar{C}\bar{N}M(\nu)]^2 \gg \bar{N} + \epsilon^2$. Then equation (A7) becomes

$$H = 4\int_0^{1/2\Delta\phi} \nu\,d\nu \ln\left\{\frac{(\bar{C}\bar{N})^2 \exp[-7.12(\Delta\rho)^2\nu^2]}{\bar{N}+\epsilon^2}\right\} \quad \text{(A9a)}$$

$$= \frac{1}{2(\Delta\phi)^2}\ln\frac{(\bar{C}\bar{N})^2\exp\left[-3.56\left(\frac{\Delta\rho}{2\Delta\phi}\right)^2\right]}{\bar{N}+\epsilon^2} \quad \text{(A9b)}$$

This is an excellent approximation to equation (A8) except when $\Delta\phi \gg \Delta\rho_l$; e.g. equation (A9b) gives the non-straight line portions of Fig. 7. The following expression gives results for the optimum value of $\Delta\phi$ that are indistinguishable (on a plot like Fig. 7) from those found from equation (A8).

$$H = n_p \ln n_i \quad \text{(A10a)}$$

$$n_p = 1/(\Delta\phi)^2 \quad \text{(A10b)}$$

$$n_i = \left\{1 + \frac{(\bar{C}\bar{N})^2\exp\left[-3.56\left(\frac{\Delta\rho}{2\Delta\phi}\right)^2\right]}{\bar{N}+\epsilon^2}\right\}^{1/2} \quad \text{(A10c)}$$

$$= \left[1 + \frac{(\bar{C}\bar{N})^2}{\bar{N}+\epsilon^2}M(\nu_s)\right]^{1/2} \quad \text{(A10d)}$$

$$\nu_s = 1/2\Delta\phi. \quad \text{(A10e)}$$

In Appendix C, we show that $\epsilon \cong 1.0$ for an array of ideal photoreceptors, i.e. those without intrinsic noise.

(A4) *Relation between* H *and the signal to noise ratio of a photoreceptor*

The mean square fluctuation σ^2_{sig} in photon counts at the photoreceptor level (ignoring noise) is found by summing the mean square fluctuations $\tilde{\sigma}^2_{sig}(\nu)$ due to individual sinusoids at each frequency. In general, $\tilde{\sigma}_{sig}(\nu)$ differs from $\sigma_{sig}(\nu)$ of equation (A3) by a constant that depends on the object power spectrum (Aseltine, 1958). Thus

$$\sigma^2_{sig} = 2\pi\int_0^{1/2\Delta\phi}\nu\,d\nu\,\tilde{\sigma}^2_{sig}(\nu). \quad \text{(A11)}$$

Similarly, the mean square fluctuation σ^2_{noise} in photon counts due to noise is

$$\sigma^2_{noise} = 2\pi\int_0^{1/2\Delta\phi}\nu\,d\nu\,\tilde{\sigma}^2_{noise}(\nu). \quad \text{(A12)}$$

Assuming that the noise power spectrum $\tilde{\sigma}^2_{noise}(\nu)$ is constant,

$$\sigma^2_{noise} = (\pi/4)n_p\tilde{\sigma}^2_{noise}. \quad \text{(A13)}$$

Since the $\tilde{\sigma}$ quantities are constants times the σ quantities, the ratio R_{sn} of mean square signal to mean square noise of the photoreceptors is

$$R_{sn} = \frac{8}{n_p}\int_0^{1/2\Delta\phi}\nu\,d\nu[\sigma^2_{sig}(\nu)/\sigma^2_{noise}(\nu)], \quad \text{(A14)}$$

where σ_{sig} and σ_{noise} are given by equations (A3) and (A4), respectively. We see by comparing equation (A14) with equation (A8) that when $\sigma_{sig}(\nu) \ll \sigma_{noise}(\nu)$,

$$H = n_p R_{sn}/2, \quad \text{(A15)}$$

i.e. the information capacity H of the photoreceptors is a simple product of R_{sn} multiplied by the number of photoreceptors per square degree of object space, when the mean square fluctuations in photon counts of the signal is below the noise level.

Optical physicists (O'Neill, 1963; Biberman, 1973) often use an expression equivalent to: $\int_0^\infty \nu\,d\nu M_l^2$ as a measure of image quality. This expression is proportional to the mean square variations in intensity on the *retina* due to a random pattern, but because of the ∞ limit rather than $1/2\Delta\phi$, differs greatly from the mean square variation in photon counts when the photoreceptors are spaced for optimum information capacity at a given intensity. This quality factor characterizes the mean square fluctuations at the photoreceptor level for those photoreceptors with $\Delta\phi \leqslant \Delta\rho_l/2$, i.e. those photoreceptors separated appropriately for detecting the highest spatial frequency passed by the lens–pupil optics. When photoreceptors are spaced at $\Delta\phi > \Delta\rho_l/2$, equation (A15) does not apply.

(A5) *Photoreceptor diameter for maximum* H

The information capacity, H, as given in equation (A10), depends upon $\Delta\rho_r$ only in as much as $\Delta\rho_r$ determines $\bar{N}$ [equation (10)] and $M(\nu_s)$ [equation (B5)]. Thus, when $\bar{N} \gg 1$ the value of $\Delta\rho_r$ that gives maximum H is the value that maximises the term $\bar{N}\,M_r(\nu_s)$. Using the exact expression for $M_r(\nu_s)$ [equation (B5)], this gives an optimum $\Delta\rho_r = 1.4\Delta\phi$. If we assume that receptors cannot overlap, then information capacity is optimum when receptors touch ($\Delta\rho_r = \Delta\phi$).

(A6) *Determination of optimum photoreceptor spacing* $\Delta\phi$ *in low intensity limit*

In general, we must resort to numerical methods to solve equation (A8) or its approximate form given by equation (A10). In the low intensity limit, $M(\nu_s) \cong 1$, and we can obtain an analytic expression for the $\Delta\phi$ that optimises H when all other quantities are fixed. We assume touching photoreceptors, i.e. $\Delta\rho_r = \Delta\phi$ and define the dummy variable q and z.

$$q = \epsilon\,\bar{C} \quad \text{(A16a)}$$

$$z = \bar{N}/\epsilon^2 = \bar{I}(\Delta\phi/\epsilon)^2 \quad \text{(A16b)}$$

$$\hat{H} = (2\epsilon^2/\bar{I})H. \quad \text{(A16c)}$$

From equation (9), with $M = 1$, we then have

$$\hat{H} = (1/z)\ln[1 + (qz)^2/(z+1)]. \quad \text{(A17)}$$

The value of z for which $\hat{H}$ is maximum is found by taking $(dH/dz) = 0$ leading to

$$\ln\left[1 + \frac{(qz)^2}{z+1}\right] = \left[\frac{z+2}{z+1}\right]\left[\frac{1}{1+(z+1)/(qz)^2}\right]. \quad \text{(A18)}$$

A good approximation to equation (A18) for the values q of interest $(0.01 < q < 1)$ is

$$z = 1.6/q, \quad \text{(A19)}$$

so that $\bar{N} = 1.6\epsilon/\bar{C}$.

The form of solution given by equation (A19) holds also when the effect of the finite photoreceptor diameter is included. From equations (A10c), $\exp[-3.56(\Delta\rho/2\Delta\phi)^2] \cong 0.7$, when $\Delta\rho_l = 0$. This additional factor of 0.7 is included in the above analysis by redefining $q = \epsilon\bar{C}(0.7)^{1/2}$ so that $\bar{N} = 1.9\epsilon/\bar{C}$.

If we ignore the effect of imperfect optics, then the value H at optimum $\Delta\phi$ is found by substituting equation (A19) into equation (A17), converting from $\hat{H}$ to H via equation (A16c). This leads to

$$H = 0.31\left[\frac{\bar{I}q}{\epsilon^2}\right]\ln\left[1 + \frac{2.56q}{1.6+q}\right], \quad \text{(A20)}$$

where $q = 0.84\epsilon\,\bar{C}$.

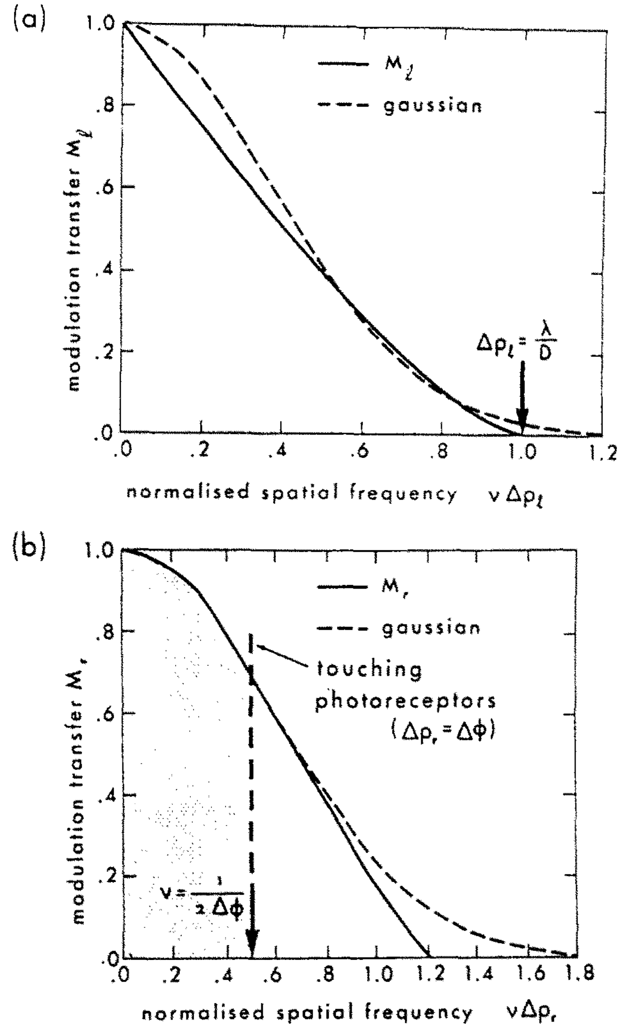

Fig. 11. The modulation transfer function for the lens–pupil M_l and the photoreceptors M_r (solid curves) compared with their Gaussian approximations discussed in appendix B. D is the entrance pupil, v the spatial frequency and $\Delta\rho_l$, $\Delta\rho_r$, and $\Delta\phi$ are defined in table 1. Note that $M_r \geqslant 0.7$, as illustrated by the shaded portion of Fig. 10b, since $v\,\Delta\rho_r \leqslant 0.5$.

(A7) *High intensity limit*

The *minimum* value of $\bar{I}$ necessary for a retina with photoreceptor spacing of $\Delta\phi = \Delta\rho_l/2$ to have maximum information capacity is found by solving equation (A10) for the optimum $\Delta\phi$ in the limit of $\bar{N} \to \infty$. This leads to

$$\ln(0.26\,\bar{N}\,\bar{C}^2) = 1.78(\Delta\rho_l/\Delta\phi)^2 \qquad \text{(A21a)}$$

$$\ln[0.26\,\bar{N}\,\bar{C}^2 M_l^2(v_s)] = 0. \qquad \text{(A21b)}$$

When $\Delta\rho_l = 2\Delta\phi$, we find from equation (A21) that $\ln(\bar{N}\,\bar{C}^2) = 8.48$ or

$$\log \bar{N}\,\bar{C}^2 = 3.68 \qquad \text{(A22a)}$$

$$\bar{N}[\bar{C}\,M_l(v_s)]^2 = 3.85. \qquad \text{(A22b)}$$

Since $\bar{N} = \bar{I}(\Delta\phi)^2$, we derive equation (10) of the text from equation (A22). We also find from equation (A21) that

$$\Delta\phi = 1.33\Delta\rho_l/[\ln(0.26\bar{N}\bar{C}^2)]^{1/2} \qquad \text{(A23)}$$

$$\cong \frac{1.33\Delta\rho_l}{\{\ln[\bar{I}(\bar{C}\Delta\rho_l)^2] - 2.7\}^{1/2}}. \qquad \text{(A24)}$$

Equation (A24) is a good approximation to $\Delta\phi$ for values of $\bar{I}$ within about 1.5 log units necessary for $\Delta\phi = \Delta\rho_l/2$.

APPENDIX B: MODULATION TRANSFER FUNCTION (MTF)

Here we present some fundamentals of the modulation transfer function MTF used in our analysis. Extensive treatises on the MTF have been given by O'Neill (1963) and Goodman (1968). For applications to the vertebrate eyes, and the human eye in particular, we refer to Westheimer (1972) and Van Meeteren (1974).

The angular intensity spread pattern I of a pupil with diameter D is given by the standard diffraction formula

$$I(X) = [2J_1(X)]/X, \qquad \text{(B1)}$$

neglecting aberrations, where $X = \pi D\phi/\lambda$, λ the wavelength of light in vacuum, J_1 the Bessel function of order 1 and ϕ the inclination to the pupil axis. The MTF is the Fourier transform of $I(X)$, i.e.

$$M_l(p) = 2[\cos^{-1} p - p(1 - p^2)^{1/2}], \quad |p| \leqslant 1; \qquad \text{(B2a)}$$

$$= 0 \qquad |p| \geqslant 1, \qquad \text{(B2b)}$$

with $p = \lambda v/D$, v is the spatial frequency in cycles per radian. Equation (B2) is given by the continuous curve in Fig. 11(a). Equation (B1) is given approximately by the Gaussian

$$I(X) \cong \exp\left(-\frac{4\ln 2}{\pi^2}X^2\right) \tag{B3a}$$

$$I(\phi) = \exp\left[-4\ln 2\left(\frac{\phi}{\Delta\rho_l}\right)^2\right], \tag{B3b}$$

which is a function of width, $\Delta\rho_l = \lambda/D$, at 50% height. The Fourier transform of equation (B3) is again a Gaussian, of the form

$$M_l(p) \cong \exp\left(-\frac{\pi^2}{4\ln 2}p^2\right) \tag{B4a}$$

$$M_l(v) \cong \exp\left[-\frac{\pi^2}{4\ln 2}(v\Delta\rho_l)^2\right]. \tag{B4b}$$

Equation (B4) is presented in Fig. 11(a) by the dashed line and is defined in the text as $M_l(v) = \exp(-3.56\,\Delta\rho_l^2 v^2)$, i.e. the MTF for the dioptrics.

We next derive an expression for the MTF of the photoreceptor M_r. Consider a photoreceptor with angular diameter $\Delta\rho_r$. The modulation transfer function of this photoreceptor then is given by

$$M_r(v) = 2J_1(\pi\Delta\rho_r v)/(\pi\Delta\rho_r v). \tag{B5}$$

Since we assume throughout the present paper that the photoreceptors are touching, $\Delta\rho_r = \Delta\phi$, where $\Delta\phi$ is the angle between adjacent photoreceptors. The maximum sampling frequency is $v_s = 1/2\Delta\phi$ so that $M_e(v_s) = 4J_1(\pi/2)/\pi \cong 0.7$. It is shown in Fig. 11(b) that, in the spatial frequency range of interest, $(0 < v < v_s)$, $M_r(v)$ is very well approximated by the Gaussian

$$M_r(v) = \exp(-1.35v^2\Delta\rho_r^2). \tag{B6}$$

Hence the MTF of the combined system of pupil–lens and photoreceptor $M = M_l M_r$ is

$$M(v) = \exp[-3.56(\Delta\rho_l^2 + 0.38\Delta\rho_r^2)v^2] \tag{B7a}$$

$$= \exp[-3.56(v\Delta\rho)^2]. \tag{B7b}$$

The Gaussian approximation is used for simplicity of presentation. It is convenient to consider the value $v = 1/\Delta\rho$, when $M = 0.03$, as the effective v where $M = 0$ so that when $\Delta\rho = \lambda/D$, the value $v = 1/\Delta\rho$ is the exact cutoff.

APPENDIX C. NUMBER OF DIFFERENT INTENSITY LEVELS n_i

When, on average, fewer than 10 photons are absorbed by a photoreceptor in one integration time ($\bar{N} < 10$), the procedure used in Section III is inappropriate for determining the number of different intensity levels. Assuming $\bar{C} = 1$, we find that $n_i = 1$ for $0 \leqslant \bar{N} \leqslant 1$; $n_i = 2$ for $2 \leqslant \bar{N} \leqslant 4$; $n_i = 3$ for $\bar{N} = 5$; $n_i = 4$ for $6 \leqslant \bar{N} \leqslant 7$; $n_i = 5$ for $8 \leqslant \bar{N} \leqslant 9$ and $n_i = 6$ for $\bar{N} = 10$. Thus, unless a minimum of two photons ($\bar{N} = 2$) is counted by at least one photoreceptor of the array, there is only one possible intensity level ($n_i = 1$) that is distinguishable with certainty. Consequently, from equation (1), the information content H of the retina is then zero. Using this last determination of n_i and equation (1), it is easy to show that *the information capacity* H *is maximized when* $\bar{N} = 2$. We are again reminded that the photoreceptors are assumed here to be without intrinsic noise and the effect of imperfect optics has been ignored.

We would like to have an expression for n_i which, when taken with equation (1), gives results for $\Delta\phi$ that are uniformly valid for all values of $\bar{N}$. This is accomplished by introducing an effective intrinsic noise of standard deviation ϵ photons, i.e. $\epsilon^2 = \epsilon_{in}^2 + k$, where ϵ_{in} is the actual intrinsic noise and k a parameter chosen to give correct results for small $\bar{N}$. We showed above that, with $\bar{C} = 1$ and $\epsilon_{in} = 0$, the information capacity H is maximized when $\bar{N} = 2$. In Appendix A6, we showed that H is maximized when $\bar{N} = 1.9\epsilon/\bar{C}$. Thus, taking $\bar{C} = 1$ and $\epsilon_{in} = 0$, we find that an effective noise of about one photon ($\epsilon \cong 1$) is required to have $\bar{N} = 2$.

Since $\sigma_{noise}^2 = \bar{N} + \epsilon^2$, we have

$$n_i = (\bar{C}\,\bar{N})^2/(\bar{N} + 1) \tag{C1}$$

for the number of different contrast levels of an array of *ideal* photoreceptors, ignoring the degrading effect of imperfect optics.

APPENDIX D. DERIVATION OF $\tilde{I}$, $\bar{N}$, AND THE CONVERSION OF $\tilde{I}$ TO TROLANDS

We let $\bar{I}$ be the mean number of photons entering the eye per square degree of object field per second. A fraction η of this number will reach the photoreceptor layer and be absorbed. Each photoreceptor accepts light from a solid angle $\pi(\Delta\rho_r)^2/4$ of object space, where $\Delta\rho_r$ is the angular diameter of the photoreceptor. If Δt is the integration or sampling time of the eye, then the mean number $\bar{N}$ of photons absorbed by a photoreceptor due to an extended object of uniform intensity is

$$\bar{N} = \bar{I}\,\eta\,\pi(\Delta\rho_r)^2\Delta t/4 = \tilde{I}(\Delta\rho_r)^2, \tag{D1}$$

where $\tilde{I}$ is defined as

$$\tilde{I} = \bar{I}\frac{\pi}{4}\eta\Delta t. \tag{D2}$$

We use the formulae of Wyszecki and Stiles (1967), p. 226, for the photopic T_p and scotopic T_s td values

$$T_p = (\bar{I}\,V_\lambda/\lambda)\,4.432 \times 10^{-11} \tag{D3}$$

$$T_s = (\bar{I}\,V'_\lambda/\lambda)\,1.138 \times 10^{-10}, \tag{D4}$$

where V_λ and V'_λ are the CIE relative luminous efficiency curves for photopic and scotopic vision and λ is the wavelength of light in vacuum in cm. We take $\eta = 0.1$ (Barlow, 1964). With $V(\lambda) = 1$, $\lambda = 5.5 \times 10^{-5}$ cm and $\Delta t = 30$ msec (Ditchburn, 1973, p. 157; Roufs, 1973), we have log T_p = log $\tilde{I} - 3.47$. With $V'(\lambda) = 1$, $\lambda = 5.07 \times 10^{-5}$ cm and $\Delta t = 100$ msec (Rodieck, 1973, p. 456; Roufs, 1972) we have log T_s = log $\tilde{I} - 3.54$. These two expressions are nearly the same so that we can use the single expression

$$\log T = \log \tilde{I} - 3.5. \tag{D5}$$

for converting from $\tilde{I}$ to trolands T. We are reminded that the ten-fold increase in (human) pupil area (Barlow, 1972) must be accounted for when converting from trolands to object world luminances.